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Palaeontological and taphonomical investigations of the exceptionally rich concentration of Miocene vertebrate coprolites from Pécs-Danitzpuszta (Hungary, Mecsek Mts.)

Zsófia Román[a], Martin Segesdi[a,b,c], Krisztina Sebe[d], Tamás Földes[e], Koraljka Bakrač[f], Attila Virág[g,h] and Gábor Botfalvai[a,d]

[a]Institute of Geography and Earth Sciences, Department of Paleontology, Eötvös Loránd University (ELTE), Budapest, Hungary; [b]Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary; [c]Department of Paleontology and Geology, Hungarian Natural History Museum, Budapest, Hungary; [d]HUN-REN-MTM-ELTE Research Group for Paleontology, Budapest, Hungary; [e]TOMOGEO Kft, Szolnok, Hungary; [f]Department of Geology, Croatian Geological Survey, Zagreb, Croatia; [g]Institute of Geography and Earth Sciences, Department of Petrology and Geochemistry, Eötvös Loránd University (ELTE), Budapest, Hungary; [h]Institute of Earth Sciences, Department of Mineralogy & Geology, University of Debrecen, Debrecen, Hungary

ABSTRACT

Thousands of coprolites have been collected from the Upper Miocene (Tortonian/Pannonian) sands of the Pécs-Danitzpuszta sand pit, one of the most important mixed Neogene vertebrate localities in Hungary. Although, the locality has been known for centuries, the coprolites have not been investigated in detail. We describe these fossils and explore their palaeoecological significance. Coprolites were examined with thin sections, X-ray powder diffraction and computed tomography. Their surface is mostly smooth, desiccation cracks were not observed. All coprolites mainly consist of apatite, indicating most probably a carnivorous diet. No evidence of herbivory has been found so far. The coprolites contain remains belonging to several groups: ostracod carapaces, bivalve shells, vertebrae from bony fishes, fish scales, as well as teeth. The CT scans show inhomogeneities in the matrix; however, in most cases they do not reliably indicate inclusions. The taphonomical features suggest rapid burial and most likely an aquatic origin. The spiral morphotype could be attributed to fishes with spiral intestinal valves. Teeth of reef-associated fish taxa indicate Badenian age for some specimens, though the coprolite assemblage might include older and younger specimens as well.

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Vertebrate coprolite; Miocene; Lake Pannon; Paratethys; coprolite taphonomy

Introduction

The study of coprolites (fossilised faeces) is a long-standing, but still constantly expanding part of palaeontology. It dates back to the 19th century, when William Buckland (1829) first identified the origin of these fossils and gave them their scientific name. Prior to Buckland (1829), coprolites were mostly interpreted as parts of fossil plants or other curiosities (see Duffin 2009 for details). According to Seilacher et al. (2001), coprolites can be regarded as conservational Lagerstätte (Konservat-Lagerstätte), as they often have a better potential to preserve inclusions than the host rock itself, making them valuable sources of palaeobiological and paleoenvironmental information (Qvarnström et al. 2016). Paleoscatology applies knowledge from recent biological studies based on the principle of actualism. However, naturally there are some limitations and in most cases, it is not easy (or nearly impossible) to assign the real producer to the coprolites, partly due to our knowledge gap on the dietary habits of some extant animals. The analyses of fossilised faeces open a window into the palaeobiology and lifestyle of extinct animals (Chin 2007; Salamon et al. 2012; Dentzien-Dias et al. 2013; Brachaniec et al. 2015; Qvarnström et al. 2017; Barrios-de Pedro et al. 2018; Bajdek et al. 2019). They are not only informative about the food preference (Chin and Gill 1996; Bajdek et al. 2014; Chin et al. 2017; Barrios-de Pedro et al. 2020b), but also the function of the digestive system and the health of an individual (Dentzien-Dias et al. 2013; Perri et al. 2017). Besides this, coprolites often contain unintentionally swallowed well preserved animal or plant fragments, which provide further information.

The sand pit of Pécs-Danitzpuszta (PDA) is a famous mixed Upper Miocene vertebrate site located in the eastern Mecsek Mts. in the Pannonian Basin, Hungary, near the city of Pécs (Sebe et al. 2021a; Botfalvai et al. 2023). The locality is unique in the extremely large numbers of coprolites collected during the last few decades (Sebe et al. 2021b and references therein). The aim of this study is to document and systematically analyse the coprolites from Pécs-Danitzpuszta. After grouping them into morphotypes, we intend to describe their mineralogical composition, the remains within, and discuss their taphonomical history as well as their palaeoecological and palaeobiological significance.

Geological and palaeontological background

Geological setting

The Mecsek Mts. are an uplifted basement block in SW Hungary, in the southwestern part of the Pannonian Basin (Figure 1). The Paleo-Mesozoic rocks are partly covered with Neogene sediments of various lithologies and palaeoenvironments (Hámor 1970; Nagymarosi and Hámor 2012; Sebe et al. 2019). The Lower to lowermost Middle Miocene, mostly clastic deposits accumulated in fluvial, then in a freshwater or brackish lacustrine environment under subtropical climate. Some volcanic rocks – lavas and pyroclastic deposits – also formed during this interval. During the Middle Miocene, in the late Langhian and Serravallian (the second half of the Badenian and in the Sarmatian), the area was part of the Central Paratethys, a major epicontinental sea of Europe (Rögl 1998; Kováč et al. 2017). After the normal marine conditions in the Badenian, the Sarmatian sea had reduced salinity, resulting in a decreased marine diversity and the disappearance of

CONTACT Zsófia Román zsofia.m.roman@gmail.com Institute of Geography and Earth Sciences, Department of Paleontology, Eötvös Loránd University (ELTE), Pázmány Péter sétány 1/c, Budapest 1117, Hungary
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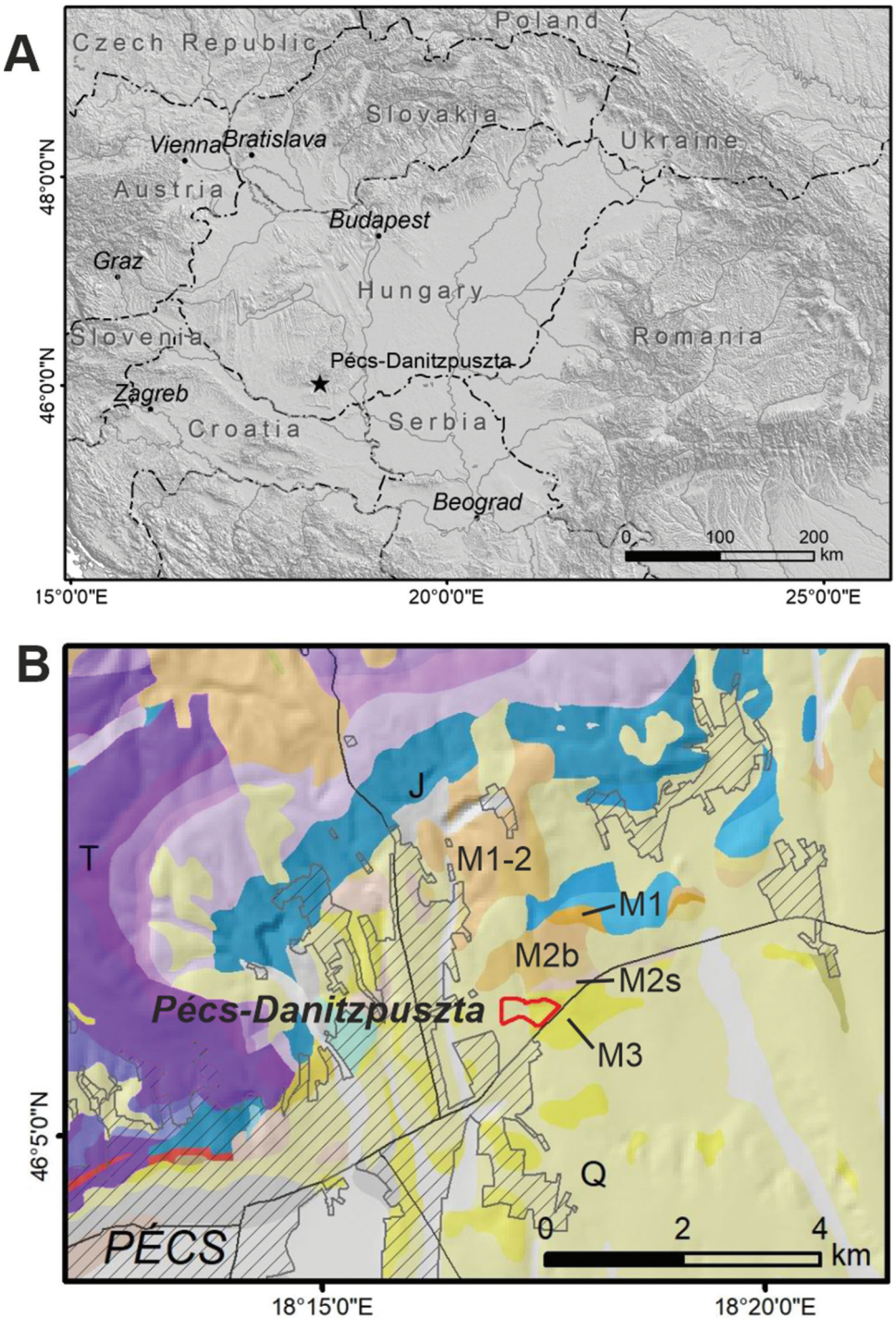

Figure 1. Geological setting of the Pécs-Danitzpuszta sand pit. (A) Location of the study area, (B) Geological map (modified from Chikán and Budai 2005). Legend: T: Triassic; J: Jurassic; M1: Lower Miocene; M1–2: Lower–Middle Miocene; M2b: Middle Miocene, Badenian (upper Langhian – lower Serravallian); M2s: Sarmatian (upper Serravallian) M3: upper Miocene or Pannonian (Tortonian); Q: Quaternary rocks.

e.g. chondrichthyans and corals. At the Serravallian/Tortonian (Sarmatian/Pannonian) boundary, the Central Paratethys basin became isolated from the world ocean, salinity further decreased and the brackish Lake Pannon formed (Magyar et al. 1999; ter Borgh et al. 2013), with carbonate-dominated offshore deposits and clastic coastal and deltaic sediments. The higher parts of the Mecsek Mts. emerged from the lake as an island until approximately 7 Ma ago (Sebe et al. 2013). After neotectonic basin inversion and uplift (Konrád and Sebe 2010) and the resulting denudation, the area was covered with loess during the Quaternary.

Pécs-danitzpuszta vertebrate locality

The sand pit of Pécs-Danitzpuszta is located at the eastern edge of the city Pécs (Figure 1(A)). It mostly exposes yellowish brown, limonitic, gravelly coarse sands (Kálla Member of the Békési Formation) that were deposited in the brackish Lake Pannon during the Late Miocene/Tortonian (Pannonian), between ~ 10.2 and 10.0 Ma (Sebe et al. 2021a; Botka et al. 2021). These sands are extremely rich in reworked fossil vertebrate remains redeposited from older Miocene stratigraphic units. The fossils include a highly

diverse assemblage of aquatic, semiaquatic and terrestrial taxa (Koretsky 2003; Kazár 2003, 2005, 2006, 2010; Sebe et al. 2021a, 2021b; Szentesi et al. 2020; Szabó et al. 2021; Szentesi 2021; and references therein). Due to the reworked state of the vertebrate assemblage only limited information is available about the exact original age of the collected fossils (Szabó et al. 2021; Botfalvai et al. 2023).

Faunal composition

The vertebrate assemblage contains various groups that could have been possible producers of the coprolites.

The most abundant remains in the sands are attributed to fishes. Szabó et al. (2021) identified 17 chondrichthyan and 12 osteichthyan taxa from the locality. The chondrichthyans are dominated by the piscivorous Odontaspididae sharks and Myliobatidae rays, whereas amongst the osteichthyans the Sparidae is the most abundant (Szabó et al. 2021). The dominant chondrichthyans, together with some reef associated taxa (Labridae and Scaridae) must be of Badenian age, as this is the only time interval when normal marine sediments accumulated in the region. The fish fauna indicates a shallow marine coastal community in a subtropical-tropical environment for the Badenian (Szabó et al. 2021). Fossils from the family of the sturgeons (Acipenseridae) and Latidae, linked to brackish and/or freshwater environments, could have originated from any Miocene stratigraphic units (Szabó et al. 2021).

Amphibians are represented by the cryptobranchid *Andrias scheuchzeri* (Szentesi et al. 2020). Based on the ecological requirements of extant salamanders (freshwater environment) and the rare earth element analyses of the remains of *A. scheuchzeri* (Botfalvai et al. 2023), a Pannonian age is inferred for this species. Amongst reptile remains, turtles are the most common, represented by three families (Trionychidae, Geoemydidae and Testudinidae) (Kazár et al. 2007; Sebe et al. 2021b). Their living relatives prefer diverse environments from terrestrial to freshwater or even brackish. However, due to the fragmentary preservation of the fossils, it is not possible to draw conclusions regarding their age. Crocodile remains are rare, only teeth have been found (Kazár et al. 2007). The low number and relatively poor preservation of the remains does not make the exact classification of the fossils possible. However, the last time that the paleoclimate was warm enough in Central Europe for crocodilians was during the late Badenian (Markwick 1998; Böhme 2003), so a pre-Sarmatian (Badenian or older) age is probable.

Cetacean (including Mysticeti, e.g. *'Cetotherium'* aff. m*aiopicum*, cf. *Cetotherium priscum*; and Odontoceti, e.g. *Acrodelphis letochae, Kentriodon fuchsii, Sophianacetus commenticius, Pachyacanthus suessi*) and sirenian (Sirenia indet.) remains of the site are most probably Sarmatian and Badenian in age (Kazár 2003, 2006, 2010; Cserpák 2018; Botfalvai et al. 2023). A phocid, *Praepusa magyaricus*, has been described from the locality by Koretsky (2003) and a Sarmatian age was suggested for it based on phylogeny. Terrestrial vertebrates have a rich record including proboscideans, rhinocerotids, tapirs, suids, equids, ruminants and carnivores (Kazár et al. 2007), but this material has not been studied in detail, so their age is unknown at the moment (Sebe et al. 2021b).

Flora

During the Early Miocene, the Central Paratethys was situated at least 200–300 km to the south of its present position (Kvaček et al. 2006). The Early Miocene (Aquitanian-mid Burgundalian/Egerian-Eggenburgian) climate was warm and humid, followed by humid subtropical conditions in the Burdigalian (Eggenburgian-Ottnangian-Karpatian) with an altitudinal difference due to the uplift of the mountains (Kováč et al. 2017). The Badenian vegetation is characterised by the decrease of thermophilous taxa and the increase of temperate taxa that could be caused by altitudinal differences between lowlands and mountains. An increased climatic gradient between the southern and northern parts of the Central Paratethys is reflected in the late Badenian floristic differentiation.

During the Early Miocene (Eggenburgian/Ottnangian) of the Pannonian realm, warm climatic conditions were documented by the flora (Ipolytarnóc assemblage) with a high number of lauraceous and other thermophilous elements, like Palmae (Erdei et al. 2007). The Karpatian flora (Magyaregregy), is comprised of a high number of thermophilous taxa, but with increasing numbers of temperate elements like *Ulmus, Acer, Rosa*, or *Salix*. Lauraceae are still a significant part of the fossil assemblage, whereas Leguminosae became abundant. In the Badenian flora of Nógrádszakál, the first mass occurrence of temperate elements during the Neogene occurred, with a higher proportion than in the older flora or even in the younger Sarmatian (late Serravallian) floras.

The Late Miocene (Tortonian/Pannonian) flora from the Mecsek Mts., Pécs-Danitzpuszta contains thermophilous elements in relatively high numbers. The dominance of lauraceous elements, and other thermophilous species, indicates the warmest conditions during the Late Miocene of Hungary. While the lakeshore lowlands were dominated by swamps, mesophytic habitats existed adjacent to the lake in the area of the Mecsek Mts. and thus in the SW Pannonian Basin at 10–11 Ma (Hably and Sebe 2016). The Sarmatian *Quercus kubinyii* indicates less wet substrate and probably has survived in the elevated areas of the Mecsek Mts., avoiding the extensive paludal-lacustrine conditions created by Lake Pannon. This area was probably a refuge, since several species that disappeared from most parts of the Pannonian Basin after the Sarmatian, found shelter here as confirmed by the occurrence of *Engelhardia orsbergensis*, a relict species in the Late Miocene of the Mecsek Mts (Hably et al. 2019).

Material and methods

During the past decades, more than seven thousand coprolites were collected from the Pécs-Danitzpuszta locality. These are housed in several collections across Hungary. The majority can be found in the József Attila City Library and Museum Collection (Komló), the Supervisory Authority for Regulatory Affairs (SZTFH, Budapest, former Geological Institute) and in the Hungarian Natural History Museum (MTM, Budapest). This study analysed 645 specimens, most of which were collected by a private collector (László Kanizsai). The coprolites were examined with a hand lens or with the use of light microscopy. The investigated coprolites are now housed and inventoried in the Vertebrate Collection of the Department of Paleontology and Geology of the Hungarian Natural History Museum. For each specimen, various parameters and characters were observed and/or measured: preservation state, morphology, colour of the specimen and the colour difference of the outer layer compared to the inner matrix (if visible), inclusions, surface texture, and the physical parameters (see Supplementary Table S1 for the list and recorded data).

Colour

Colour data recording used a four-step relative scale defined on the basis of the two extremes of the colours of the specimens (Figure 2A). The lightest coprolites (Figure 2A/a), the yellowish (Figure 2A/b), the light brown (Figure 2A/c) and the darkest specimens (Figure 2A/d) are similar in colour to the ones pictured in Figure 2A. If the coprolites were not of uniform colour, they were

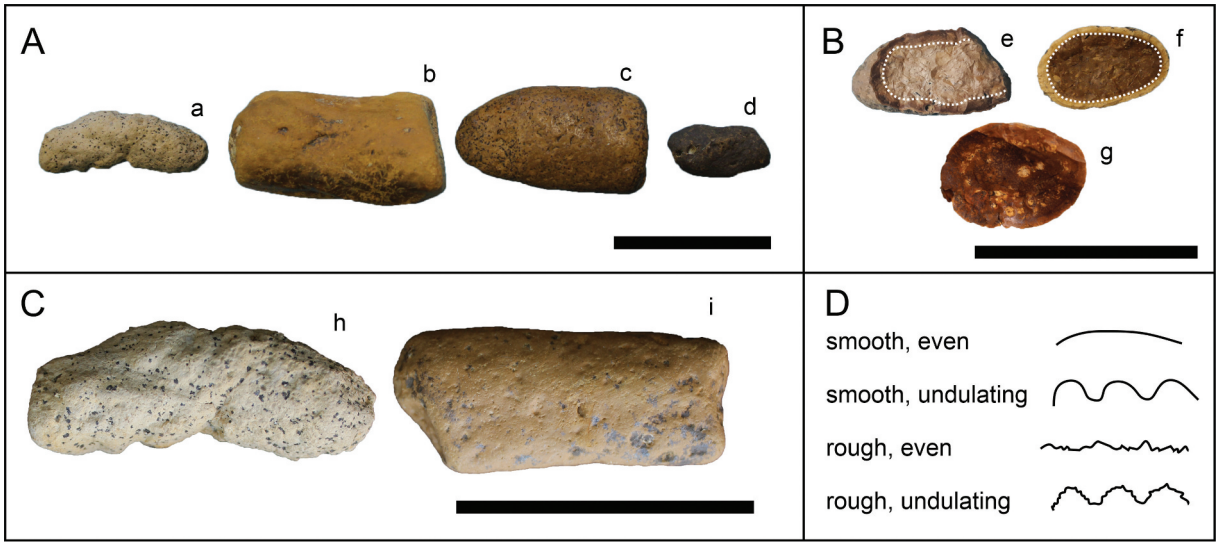

Figure 2. The characters used in describing the coprolites. (A) the colours of the coprolites, a) the lightest coprolites (PAL 2022.60.1), b) yellowish coprolites (PAL 2022.74.1), c) brown coprolites (VER 2022.593), d) the darkest coprolites (PAL 2022.80.1), (B) the relative colour difference of the outer layer, e) outer layer is darker (PAL 2022.83.1), f) outer layer is lighter (PAL 2022.79.1), g) no visible difference (PAL 2022.89.1), (C) coprolites with different surface textures, h) (PAL 2022.60.1), i) (PAL 2022.59.1), (D) the surface textures, scale bar is 5 cm.

placed into a group based on the colour that covered most of the surface. Some coprolites have a differently coloured outer layer: the documentation of this feature was based on the relative colour difference with the inner matrix (Figure 2B).

Morphology

Based on the morphology, the coprolites were separated into different groups. These groups were created with the aim of investigating whether it is possible to link the coprolites to different taxa, because the morphology is considered to be of taxonomic importance (e.g. McAllister 1985). Furthermore, by recording the morphology together with other parameters, we had the opportunity to investigate whether there is a relationship between the other parameters and/or possibly the age of the specimens.

Surface texture

The surface texture of the coprolites was classified based on roughness (Figure 2C,D). Smooth-surfaced coprolites have been separated from rough-surfaced ones. The evenness (such as undulating or even) of the surface was also recorded (Figure 2C,D).

Mineralogical composition

By examining the composition of a coprolite, it is possible to detect mineral phases that may have been derived from food processing or formed in processes unrelated to the organism. Prior to the mineralogical analysis the surface of the coprolites was cleaned with a wet toothbrush. One specimen per morphotype was randomly selected for the investigation. Samples were taken from more than one location on the fossils. In the case of one two-coloured coprolite, the darker outer layer was sampled separately from the whitish inner matrix. Samples were ground, and the top-loaded powder samples were investigated with powder X-ray diffraction (Cu-Kα source, 45 kV, 35 mA, $\lambda = 1.5406$ Å, 0.05° 2Θ step, 2 s detection time) at the Department of Mineralogy of the Eötvös Loránd University (ELTE, Budapest). The Bruker DiffracPlus EVA software was used for the evaluation of diffractograms. During the destructive study we aimed to keep at least half of each coprolite for further analysis.

CT scanning

CT scans were recorded at the University of Pécs Clinical Centre with a Siemens Somatom Perspective instrument (resolution: $0.18 \times 0.18 \times 0.6$ mm, kernel: 180 s, pitch factor: 1, feed/rotation: 38.4, tube current: 220 mA, tube voltage: 130 kV). Twenty-three specimens were selected based on their larger size and/or visible inclusions. The analysis of the scans was carried out with the RadiAnt DICOM Viewer software.

Thin sections

Thin sectioning is an effective tool for studying the internal structure or inclusions within a coprolite that are not visible to the naked eye. Ten coprolites from several morphotypes (both with and without visible macroscopic inclusions) were selected. Preparations were made in the Department of Paleontology (ELTE). Coprolites were embedded in synthetic resin (Araldite 2020, with the titre of 100:30). After impregnating the cutaway surface with synthetic resin, they were polished with SiC powder (standard grain sizes: 320, 600, 1000). The samples were then fixed onto glass plates, after which, the cutting and polishing of the other side was done. The thin sections were examined using a Nikon Eclipse LV100Pol polarisation microscope equipped with Image-Pro Insight 8.0 software and a QImaging Micropublisher 5.0 RTV digital camera.

Palynology

Palynological analyses were carried out on six coprolites of three different morphotypes (elongated, cylindrical and spiral). Standard palynological processing techniques were used to extract the organic matter (e.g. Moore et al. 1991; Wood et al. 1996). Slides were mounted in glycerine and examined using a Leica DM2500 transmitted light microscope combined with the interference contrast. Photomicrographs were taken using a Leica MC190 HD camera connected to the Leica LAS EZ software.

The palynofacies analyses of the organic matter were performed according to Tyson (1995). Coexistence Approach (CA) method, introduced by Mosbrugger and Utescher (1997) was applied but only on the one palaeoclimatic parameter – Mean Annual Temperature (MAT) with caution due to the insufficient number of sporomorphs. Palaeoclimatic estimations obtained are based on climatic requirements. These values of the coexistence intervals have been taken from the palaeoflora database (http://www.palaeoflora.de).

Results

Morphology

In the PDA assemblage nine morphotypes have been distinguished. They are as follows: (Figure 3):

Elongated
The width along the longitudinal axis is roughly constant. The ends are rounded.

Cylindrical
They have a circular cross-section, the width along the longitudinal axis is constant. The surface of the ends is flat.

Conical
The diameter increases throughout the longitudinal axis; some have a constriction towards the thinner, sometimes pointed end.

Spiral
The faeces are twisted around their longitudinal axis. The whorls vary in number, but are evenly spaced along the entire coprolite.

Flat
The dimension of one axis is significantly smaller than the others, outline varies, edges are rounded.

Sinuous
A sequence of bumps, separated by constrictions is visible along the longitudinal axis on both sides of the coprolite.

Curved
The longitudinal axis of the coprolite is curved, the width along the longitudinal axis is roughly constant, the ends are rounded.

Spherical
All the axes of the coprolite are roughly the same size.

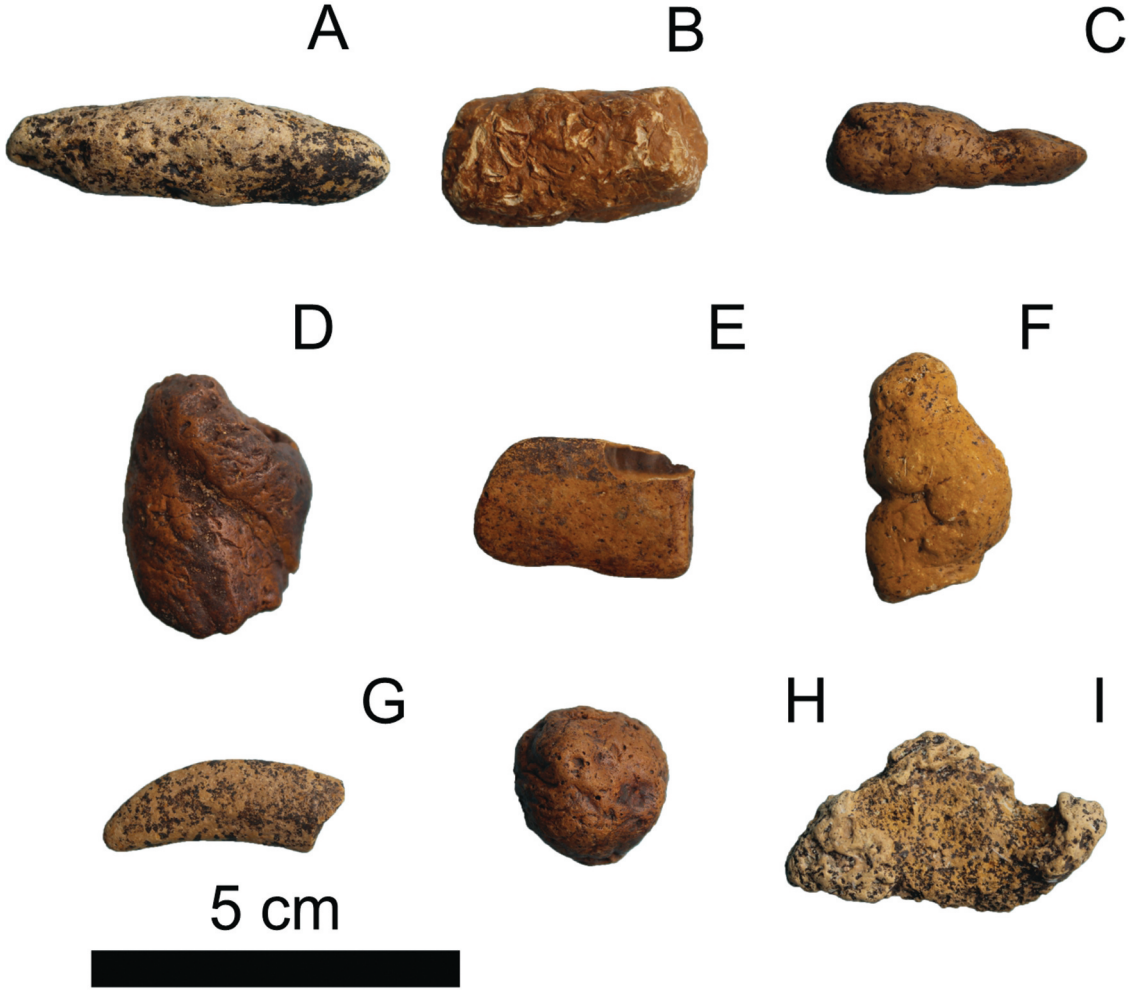

Figure 3. Vertebrate coprolite morphotypes from the Miocene Pécs-Danitzpuszta vertebrate locality. A) elongated (PAL 2022.71.1), B) cylindrical (PAL 2022.90.1), C) conical (PAL 2022.70.1), D) spiral (PAL 2022.81.1), E) flat (PAL 2022.63.1), F) sinuous (PAL 2022.72.1), G) curved (PAL 2022.68.1), H) spherical (PAL 2022.73.1), I) irregular (PAL 2022.57.1).

Irregular

This assembly includes all coprolites that have not been grouped into one of the defined morphotypes, presenting no definite shape.

Within our sample of 645 specimens, the nine recognised morphotypes clustered in the following proportions: elongated (52%), irregular (21%), cylindrical (10%), conical (5%), spiral (4%), flat (3%), sinuous (2%), curved (2%) and spherical (1%). The spiral coprolites seem to have been twisted around their longest axis: in some cases, the coiling can clearly be seen along the entire specimen (Figure 3D), in others the spiral pattern is less obvious. In some spiral specimens (PAL 2022 81.1; PAL 2022 89.1), the spiral pattern was not visible after the coprolite was broken or in the thin sections.

Size

The size of the coprolites along their major axis varies between 1–9 cm (Table 1). However, some specimens are clearly broken, these were excluded from the analyses.

The length and diameter of the individual coprolite morphotypes (Figure 4) tend to follow a lognormal distribution, which is one of the most frequently observed distributions in nature and describes a large number of physical and biological phenomena (Bergmann and Bill 2008). According to the results of Shapiro-Wilk tests (implemented by the default shapiro.test() function of the R programming environment), their logarithm does not differ significantly from a normal distribution on at least a 90%, but often higher significance level.

Colour

The colour of the coprolites ranges from almost white to dark brown (Figure 2A). Most of them are not a uniform colour, but rather spotted. Among the coprolites the light brownish are the most abundant (35%), closely followed by the yellowish (33%), the lightest (18%) and the darkest coprolites (14%). In summary the lighter and the darker coprolites are about equally represented.

Surface texture, taphonomical features

Small pits and somewhat larger dents are common features on the surface of the coprolites (Figure 2C). A few specimens have sediment particles adhered to their surface. As a general trend, both smooth and rough surfaced specimens are present in all of the morphotypes. The smooth-surfaced coprolites represent the majority in all of the morphotypes with the exception of the spherical. Three groups (sinuous, curved and spherical) show the least

Table 1. Descriptive statistical parameters of the measurements (based only on whole specimens) for each morphotype of the coprolites. Values are given in millimetres.

		elongated	irregular	cylindrical	conical	spiral	flat	sinuous	curved	spherical
	n.	295	122	60	34	22	20	13	11	4
length										
	minimum	18	16	16	21	23	23	28	24	19
	maximum	82	78	66	45	60	55	51	57	22
	median	42	33	33.5	30	39	39	41	34	20
	mean	42.96	33.36	35.23	31.06	39.41	38.75	41.08	36	20.25
	standard deviation	10.39	9.84	10.23	6.59	9.83	8.83	7.09	8.61	1.5
diameter										
	minimum	7	10	7	8	13	9	14	10	15
	maximum	44	38	35	22	28	37	30	46	21
	median	17	17.5	15	12.5	16	20	20	16	16.5
	mean	18.04	18.7	16.28	13.09	17.86	21.5	20.77	18.36	17.25
	standard deviation	5.45	5.67	4.89	3.7	4.68	6.74	4.85	10.05	2.87

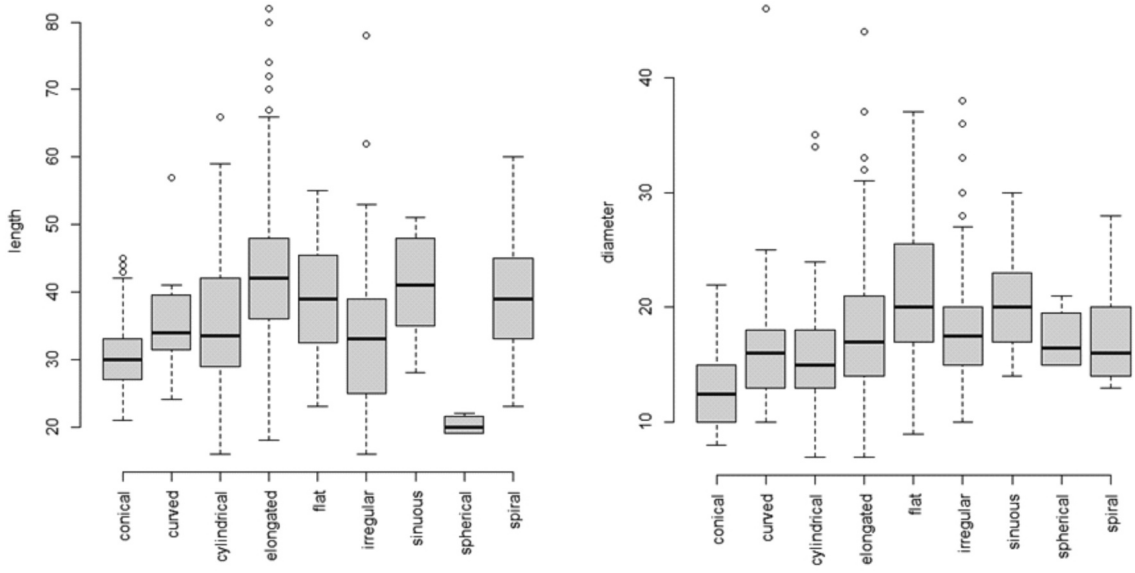

Figure 4. Box and whiskers plots of the basic measurements by coprolite morphogroups.

amount of difference in the proportion between the two categories. Almost seventy percent (69%) of the specimens have an undulating surface. All morphotypes have both undulating and even surfaced coprolites, except the spherical, which has only specimens with an undulating surface. All of the morphotypes, except for the flat specimens, have more specimens with an undulating surface texture than with an even surface texture. Drying cracks were not detected on the observed specimens. Some of the coprolites have a flattened side, clearly overprinting the original morphology.

Mineralogical composition

The results from the mineralogical analysis show that all of the samples taken are phosphatic, with the mineral apatite being the main component, regardless of the morphotype and colour of the specimen. Goethite was also detected in all the samples. The diffractograms recorded from PAL 2022.78.1 show that only the outer darker part of the matrix had a detectable amount of goethite in the mineralogical composition, whereas the inner part was clearly apatitic (See Supplementary 1).

Inclusions

Most of the observed coprolites have no or very few identifiable inclusions on their outer surface. However, the broken surfaces of some specimens present abundant remains. Four analysed coprolites contained mollusc fragments (See Supplementary Table S1). These were generally fragmented and poorly preserved (Figure 5A), or in some cases only an external mould was present (PAL 2022.58.1). Bivalve fragments were observed in three coprolites, they all show radial ribbing, but the poor state of preservation does not allow for further identification. The mould of a single gastropod was also identified (Figure 5B), but a detailed taxonomic identification was not possible due to its poor preservation. Additionally, two coprolites contained ostracod remains, one (PAL 2022.56.1) in which the valves were unidentifiable (Figure 5C), and in another (PAL 2022.81.1) just one valve was seen in a single thin section.

The most abundant remains in the studied coprolites are vertebrae from different animals. These have an hourglass or a curved shape with protruding spines. The hourglass shape is characteristic of amphicoelous vertebrae of fishes and amphibians. The vertebrae observed on the external surface of the specimens are fewer in numbers; their sections are less characteristic, and their surface is weathered. Furthermore, the remains of teeth belonging to at least three different fish taxa were observed in some coprolites. A *Calotomus* sp. tooth plate (Figure 6A), similar to the one figured by Szabó et al. (2021, Plate XIII: I, J; CSERPÁK F. coll., inv. nr.: Dp3923), but less complete and in a somewhat worse state of preservation was observed in one of the coprolites. The characteristic flat teeth of Sparidae are present in a few specimens (Figure 6B,C). A tooth belonging to the Labridae (Figure 6D) was also observed, along with coprolites containing some unidentifiable teeth. The teeth have a similar state of preservation as those reported from the Danitzpuszta locality (Szabó et al. 2021). All of the preserved

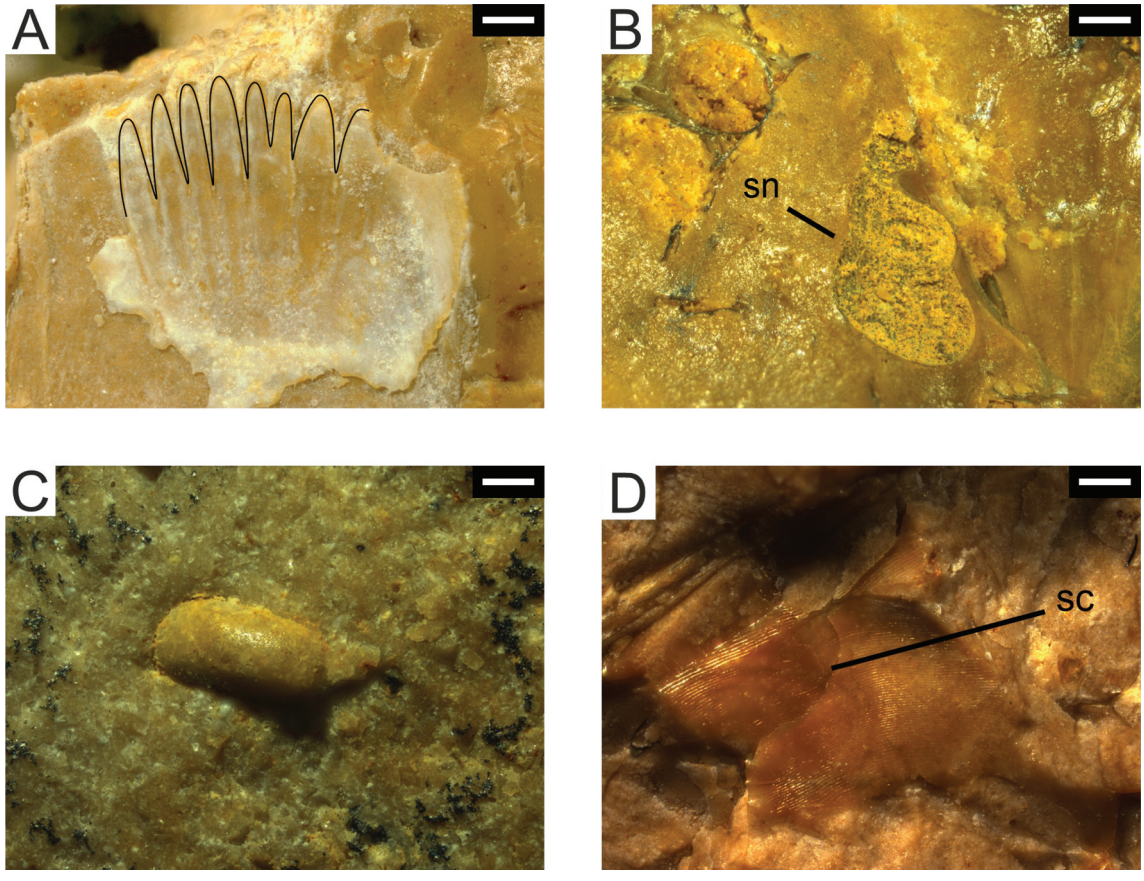

Figure 5. Inclusions from vertebrate coprolites. (A) unidentified mollusc (PAL 2022.67.1), (B) gastropod (sn) external mould (PAL 2022.66.1), (C) ostracod remain (PAL 2022.56.1), (D) fish scales (sc) (PAL 2022.83.1), scale bar is 0,3 mm.

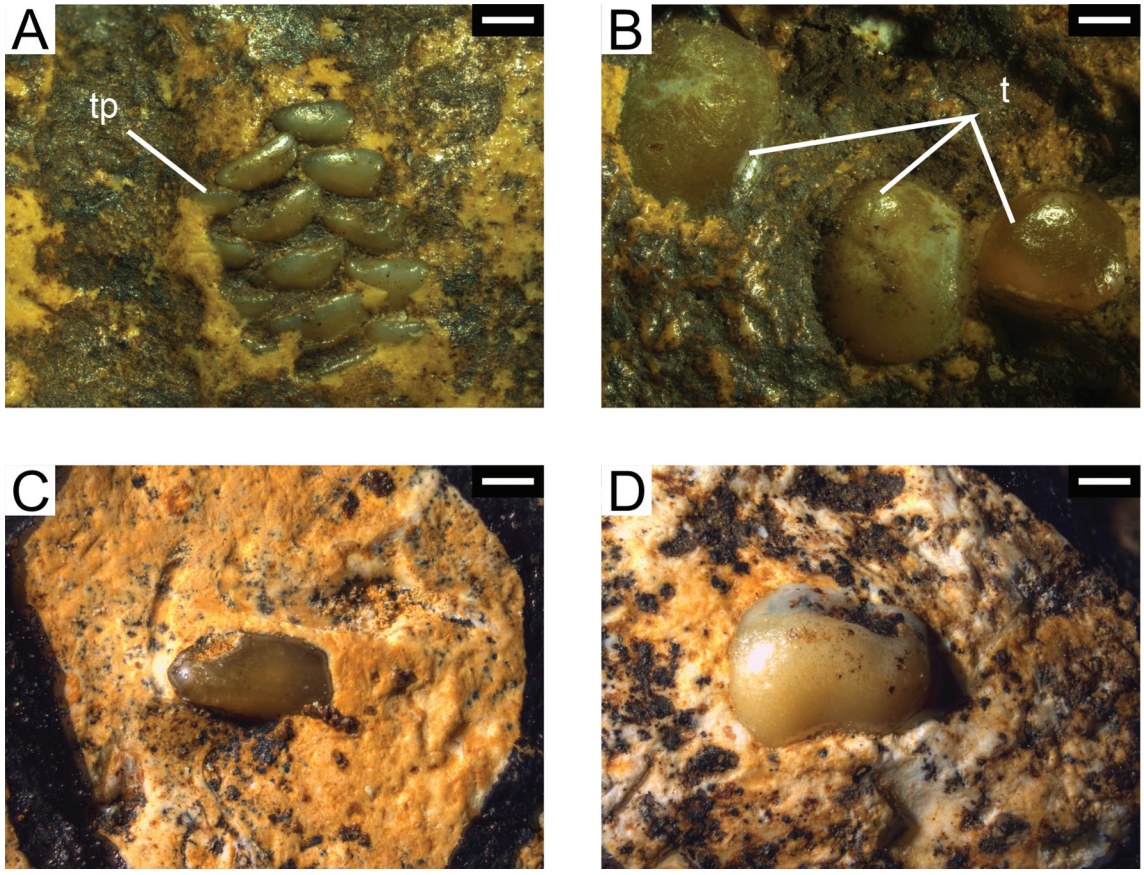

Figure 6. Fish teeth from vertebrate coprolites. (A) *Calotomus* sp. tooth plate (PAL 2022.55.1), (B-C) Sparidae (PAL 2022.77.1, PAL 2022.69.1), (D) Labridae (PAL 2022.61.1), scale bar is 0, 3 mm.

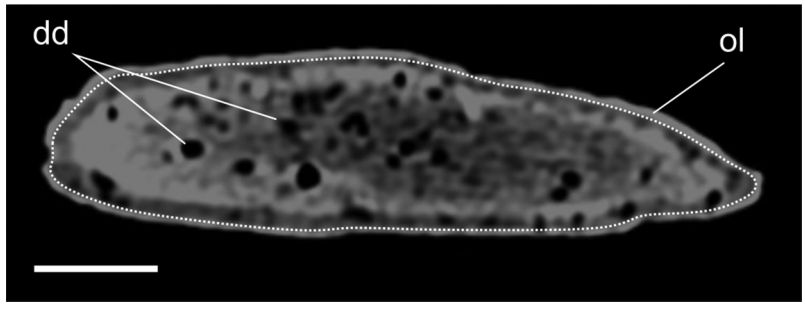

Figure 7. CT scan from a vertebrate coprolite, with macroscopically visible inclusions. (PAL 2022.58.1) (dd) density difference, (ol) outer layer, scale bar is 1 cm.

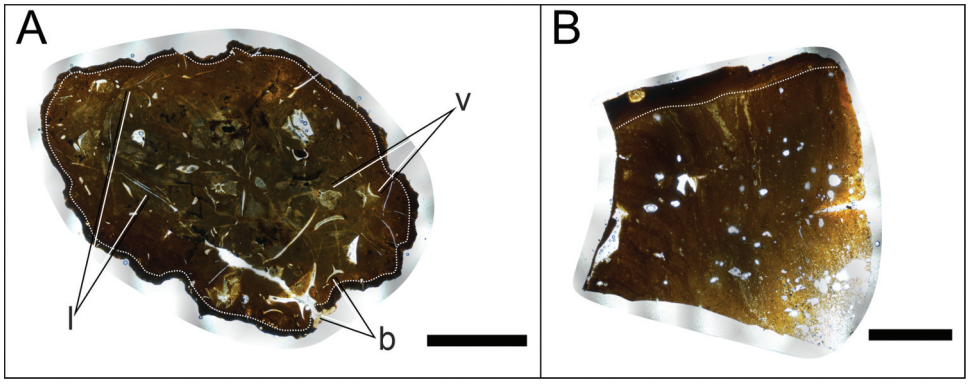

Figure 8. Two different coprofabrics. (A) inclusion rich coprofabric with vertebrae (v), lamellar inclusions (l) and bone fragments (b), (B) inclusion free coprofabric, scale bar is 5 mm.

teeth have intact layers of enamel. Fish scales were also found within the observed coprolites, but their poor state of preservation did not allow their taxonomic identification.

CT scanning

The majority of the CT scans showed a large number of isometric density differences within the coprolites (Figure 7). However, these were not indicative of real inclusions. Additionally, the scans of coprolites with and without macroscopic inclusions looked strikingly similar. The differently coloured outer layer was clearly visible on the scans (Figure 7). To date, CT scanning did not prove to be an effective tool for identifying inclusions in the case of the PDA coprolites.

Thin sections

Two widely different coprofabrics were distinguished in thin sections (Figure 8). The first had a large number of inclusions (Supplementary Figures S2–9), whereas in the second, the remains of ingested food was completely absent (Supplementary Figures S10–11).

The inclusion-free coprofabric exhibits a mostly homogenous, fine-grained groundmass, without any recognisable inclusions.

The inclusion-rich coprofabric exhibits a mostly homogenous, fine-grained matrix and a large number of inclusions. This coprofabric contains mostly vertebrae, generally 0.2–2 mm in size. Apart from vertebrae, other inclusions with an internal structure comprised of almost parallel 20–30 µm long structures were interpreted as bone fragments (Supplementary Figure S12). There are also some thin lamellar inclusions and some unidentifiable fragments. Two slightly different versions of this coprofabric can be distinguished. Sections made from two specimens (Supplementary Figures S4, 5) contain a large number of tiny, very fragmentary, and therefore unidentifiable inclusions plus a few larger ones. The rest of the sections contain a higher proportion of larger inclusions (Supplementary Figures S2, 3, 6–9).

A number of irregularly shaped spots are visible in the matrix of a coprolite (Supplementary Figure S11). In some cases, they have a light-coloured bordering ring around them, but these are not connected to inclusions. Both the spot and the rest of the matrix are fine-grained.

Palynology

The analysed coprolites contain very little organic residue (Figure 9). Palynofacies is dominated by phytoclasts. Palynomorph concentrations are very low, ranging from 39 to 770 palynomorphs per gram (ppg). The dominance of pollen of one genus in each coprolite was observed in the analysed material (Table 2).

In coprolite D-1 are very rare pollen grains with a slight dominance of *Carpinus* pollen, somewhat scarcer *Pinus* pollen, and individual pollen of *Quercus*, *Carya*, *Artemisia*, *Plantago* and pollen from the Cichorioideae. In D-2 are also rare pollen grains with a predominance of *Hedera helix* pollen and individual pollen grains of *Betula*, *Pinus*, *Plantago*, Cichorioideae and cf. *Juniperus*. Coprolite D-3 has rare pollen grains with an increased proportion of *Quercus robur*. Pollen of *Pinus* and *Carpinus* are also present. In D-4 are only a few pollen grains of *Quercus robur* and individual pollen of *Juniperus*, *Picea* and Caryophyllaceae. Coprolite D-5 has infrequent pollen grains with a predominance of *Pinus* and Poaceae grass. Lastly, coprolite D-6 preserved very rare pollen grains with a slight dominance of *Taxodium* and *Pinus*, *Pterocarya*, *Betula*, *Hedera helix*, *Poaceae* and cf. *Juniperus*.

Discussion

Coprolites from the Miocene

Vertebrate coprolites are known from all geological periods, beginning in the Ordovician (Hunt and Lucas 2012). The majority of the published coprolite materials is limited to the Mesozoic, focused mainly on Cretaceous specimens (e.g. Vajda et al. 2016; Barrios-de Pedro et al. 2018, 2020a, 2020b; Rummy et al. 2021; Chin et al. 2017; Eriksson et al. 2011; Prasad et al. 2005; Schwimmer et al. 2015; Segesdi et al. 2017; Qvarnström et al. 2019 and references therein), whereas occurrences of Miocene coprolites are less well known.

Abella et al. (2021) pointed out that the vast majority of Miocene coprolites is either produced by bone cracking large hyaenas (Hyaenidae) or Borophaginae canids. Concentrating only on the Miocene of Europe, there is some scattered record of coprolites. See the following short summaries:

Antunes et al. (2006) described three coprolites with ungulate footprints from the sandpits in, or close to Lisbon, Portugal. Two of the footprints were possibly made by the producers themselves. Although no detailed description of the other coprolites from the localities is given, the authors mention that sometimes coprolites were found in large numbers, and several 'types and sizes' are present. The coprolites are assigned to the producer based on the size and the shape.

Peñalver and Gaudant (2010) provided information about small coprolites produced by fishes in The Bicorb paleolake in Spain. The authors separated two types, mostly based on the contents (insect remains or miliolid foraminifera) and size of the fossils. The coprolites are assigned to the producer based on: (1) the inclusion being remains of small aquatic organisms, (2) the consistent size of the excrement with that of extant *Aphanius* fishes, the only aquatic vertebrates found within the sites. Both types of coprolites could have been produced by the same producer based on seasonal prey availability.

Pesquero et al. (2011) reported around a thousand hyaena coprolites from the La Roma 2 fossil site from Spain. The coprolites came from the fossil bearing grey clay marls, interpreted as a marginal lacustrine environment with episodic flooding events and external lutitic supplies. The coprolites are assigned to the producer based on: (1) the evidence of heavy digestion on the bone fragment inclusions, (2) the consistent shape and size with extant spotted hyena faeces, (3) the phosphatic chemical composition and (4) the presence of only two identified carnivorous taxa at the site, both belonging to the Hyaenidae.

Collareta et al. (2019) described a large vertebrate bitten spiral coprolite from the marine calcareous deposits of the Pietra leccese (southern Italy). The specimen was likely produced by a shark based on: (1) the large size together with the spiral morphology and (2) the chemical composition. The biting animals were identified as a shark and most likely a bony fish. Additionally, Collareta et al. (2022) described a grazing trace of a sea urchin on the same specimen.

Abella et al. (2021) reported two coprolites from Batallones-3, a pseudokarst natural carnivore trap, Madrid, Spain. The remains are found as fossiliferous breccia in marls deposited in the cave. The coprolites are assigned to their amphicyonid and basal hyaenid producers based on: (1) the size and the relative completeness of the bone fragments within them, (2) the consequent food-processing mechanisms related to the putative producers and

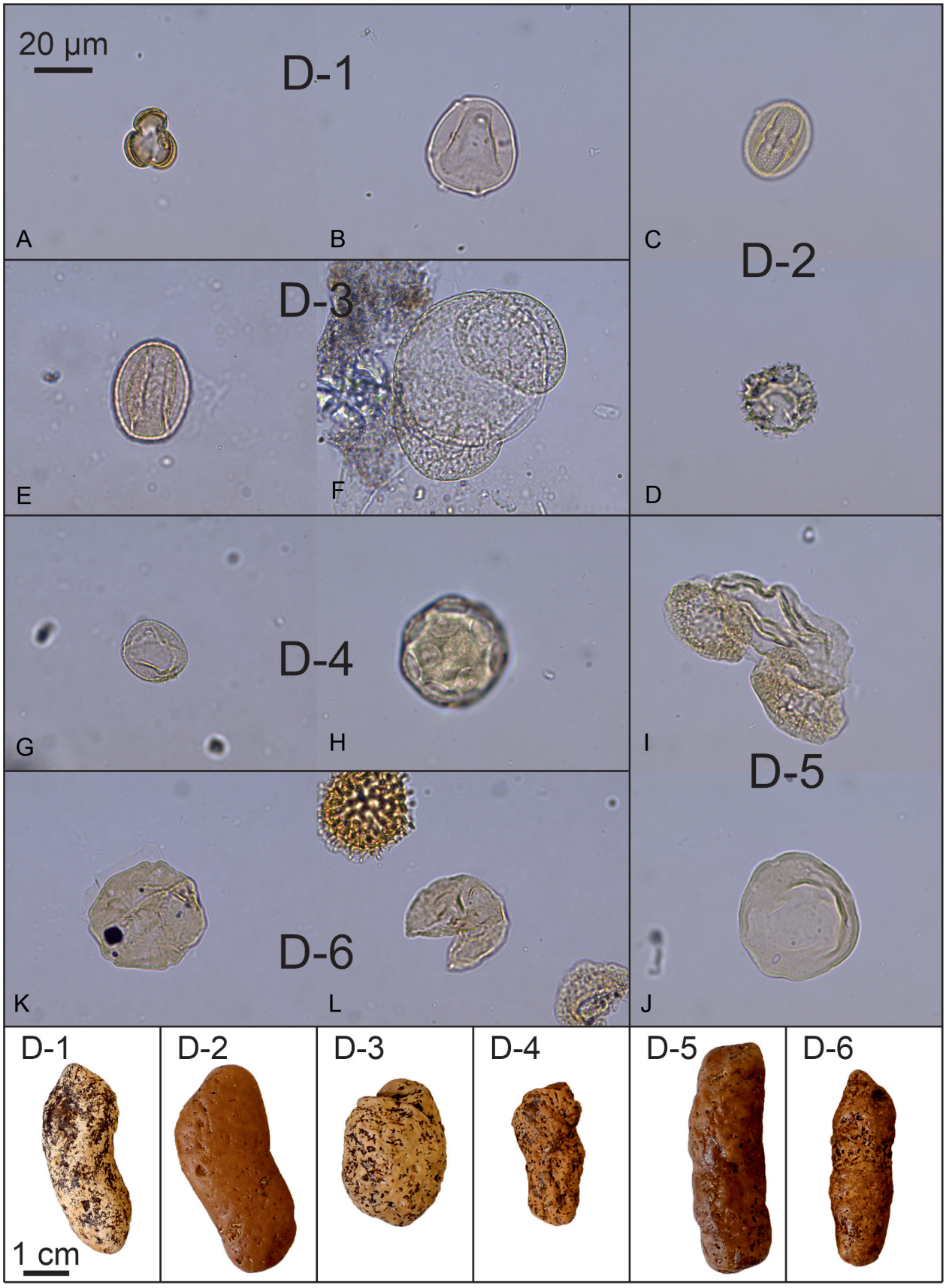

Figure 9. Pollen from coprolites: D-1: A) *Artemisia* B) *Carpinus*, D-2: C) *Hedera helix*, D) Cichorioideae, D-3: E) *Quercus robur*, F) *Pinus*, D-4: G) *Juniperus*, H) Caryophyllaceae, D-5: I) *Pinus*, J) *Carya*, D-6: K) *Pterocarya*, L) *Taxodium*.

Table 2. Palynological results from the coprolites D-1 to D-6.

sample	*Pinus* sp.	*Picea* sp.	*Taxodium* sp.	*Quercus ilex*-type	*Quercus robur*-type	*Carpinus* sp.	*Betula* sp	*Carya* sp.	*Pterocarya* sp.	*Juniperus* sp.	*Hedera* sp.	Asteraceae tubuliflorae	Asteraceae liguliflorae	*Plantago* sp.	Poaceae	*Artemisia* sp.	Caryophyllaceae	Unidentified	ex. *Lycopodium*	mass (g)	Ls (18584)	pollen-sum	concentracion	MAT (mean annual temperature) °C
D-1	2			1		8		1				1	1	1		1		2	1112	10.57	2	18	57	5.3–17.6
D-2	1					1	1			1	74		1					1	327	15.44	2	80	589	7.6–18.3
D-3	1				23	1				3								1	184	17.21	2	29	340	5.3–15.7
D-4		1			2					1							1	2	273	7.48	2	7	127	2.6–15.7
D-5	76							2							6			2	313	13.26	2	86	770	4.4–25.5
D-6	2		7		1				1	2	1				2			8	2691	8.53	2	24	39	13.3–18.1

their dentition, and also (3) the size and morphology of the coprolite.

Brachaniec et al. (2022) investigated 10 excrement shaped siderite masses, interpreted as coprolites from the Miocene of Poland. The putative tortoise (Testudinoidea) and snake (Serpentes) produces were assigned to the coprolites based on (1) the morphology compared to a large number of excrements of extant fish, amphibians, reptiles, birds and mammals and (2) the very limited number of inclusions.

Gross et al. (2023) described 18 specimens from a vertebrate fossil-rich paleosol at the Gratkorn site (Serravallian/Sarmatian), Austria. The coprolites were assigned to hyaenid and barbourofelid producers based on the (1) morphology, size, (2) microstructure and inclusions and (3) the fossil record known from the site.

Outside of Europe, there are also some descriptions of coprolites from the Miocene. Wetmore (1943) described feather impressions in a coprolite from Maryland, U.S.A.. The feathers seemed to be contour feathers from an aquatic bird. The author assumed that the coprolite must have been produced by a large fish or a crocodile, based on the predators for birds known from the deposits.

Godfrey and Smith (2010) reported two shark bitten coprolites from the Calvert Cliffs outcrop belt along the Chesapeake Bay in Maryland, U.S.A.. The authors state that coprolites from the area are not common, but some in situ and float specimens are found in the cliffs and on the beaches below the cliffs. The producer(s) of the fossils are unknown, except for one specimen with detailed tooth impressions, where the identification of the biting animal (*Galeocerdo* sp.) was possible based on the Miocene shark taxa known from the locality.

Dentzien-Dias et al. (2018) studied 106 specimens from five localities, from the Urumaco Formation, Venezuela. The authors described five morphotypes, the size of the fossils ranges from 17 to 200 mm in length. The coprolites were assigned to the following producers: rodents, toxodontids, crocodilians, undetermined carnivorans or perhaps mammals and sirenians. Determination of the producers was based on: (1) the calcium phosphate composition of the fossils, typical for carnivores, (2) the presence of vegetal inclusions in great proportions in certain morphotypes, (3) the morphological similarity of the coprolites with the faeces of extant animals, (4) the co-occurrence of putative producers body fossils together with the coprolites, and (5) the similar excrement content and the preservation state of the inclusions within the scat of extant animals.

Wang et al. (2018) examined 14 *Borophagus* coprolites from two localities in the Turlock Lake area, Mehrten Formation, California, U.S.A. The coprolites are assigned to the producer based on: (1) the large number of bone fragments in them and their rounded, acid etched nature, (2) the large size of the fossils and (3) their morphology.

Tomassini et al. (2019) studied 111 Sparassodonta coprolites originating from three localities from Patagonia, Argentina (Burdigalian-Early Langhian). Based on the size and morphology, two morphotypes were distinguished. The coprolites are assigned to the producer based on: (1) morphology and (2) size, (3) chemical composition and bone and tooth remains within the fossils, (4) taphonomy of the bone remains.

Godfrey et al. (2022) reports three burrowed vertebrate coprolites from the Calvert Formation, Plum Point Member (upper Burdigalian – most of the Langhian). Based on their large size and shape, the crocodilian *Thecachampsa* sp. was suggested as the most likely producer.

There are numerous publications on Quaternary coprolites (see Hunt and Lucas 2012). A branch of coprolite research is devoted to the study of these coprolites, which often have not undergone diagenesis.

The coprolites described by Peñalver and Gaudant (2010), Tomassini et al. (2019) and Gross et al. (2023) as well as one specimen by Antunes et al. (2006) are similar in age to the Pécs-Danitzpuszta specimens but were deposited in a different paleoenvironment. Collareta et al. (2022) and Godfrey et al. (2022) reported coprolites from a similar age and a locality with a similar fossil assemblage, including sharks, rays, cetaceans (Mysticeti and Odontoceti), seals, sirenians and crocodilians. Although the age and the composition of the fauna is similar to Pécs-Danitzpuszta, the number of coprolites collected from the latter location is significantly higher.

In conclusion, the PDA coprolites are unique among other Miocene coprolites both in the extremely large number of coprolite specimens found and also the depositional environment.

Origin of the coprolites

The PDA coprolites represent a range of sizes (from 1 to 9 cm). The size of coprolites is thought to be very informative by some researchers, as the size of the excrement is usually positively correlated with the size of the producing animal (Chin 2002). However, this rule of thumb is not true in the reverse, as large animal can produce small scats as well. Coprolites larger than 4–5 mm are generally regarded as produced by vertebrates (Thulborn 1991).

Colour and mineralogical composition

The colour of the PDA coprolites did not help separate the specimens by age. The purpose of studying the mineralogical composition was to detect mineral phases related to food processing, and also those that formed in processes unrelated to the organism. Determining the type of the cementing mineral helps to isolate apatite-rich coprolites produced by carnivorous animals (Chin 2002). The main composition of the PDA coprolites was apatite, regardless of the morphotype and colour of the specimens. For the coprolite where the inner matrix was sampled separately from the outer layer, the former was composed of apatite, whereas the latter also had a detectible amount of goethite. The phosphorus present in the carnivore excrement is mostly dietary; since its source is the bioapatite forming bones and teeth as well as the phosphorus contained in soft tissues (Uribarri 2007). The high phosphorus content of the investigated coprolites indicates producers consuming food of animal origin (Thulborn 1991; Hollocher et al. 2005).

Coprolites clearly originating from herbivorous animals have not been found in the investigated material. Although herbivorous animals greatly outnumber carnivores in most terrestrial ecosystems, their coprolites are less frequently found (Chin 2007), because scat produced by herbivores contains a higher quantity of residual nutrients. These are often exploited by coprophagous animals, and this results in the disintegration of the faeces (Chin and Gill 1996). Furthermore, the preservation of herbivorous faeces requires cementing material from external sources, whereas carnivore scat already contains calcium and phosphate, which can precipitate into apatite, thus providing a cementing material (Chin 2002).

The goethite content probably has an external source and can be attributed to the limonitic impregnation affecting the host sand and most of the vertebrate fossils of the PDA (Sebe et al. 2021a).

Depositional environment

No desiccation cracks have been observed on the surface of the coprolites. This does not necessary indicate an aquatic origin, given that the producers might have had terrestrial lifestyles and their excrement was quickly transported into water. However, this appears as less likely; as undried faeces would have probably been disintegrated during transportation. We have no recent analogies for the aquatic transport of such non-dried faeces.

Some specimens have a flattened surface, which could have resulted from the spreading of faeces after defaecation or from the contact with the substrate at the moment of defaecation or upon arrival on the ground, depending on the consistency of the faeces (Thulborn 1991). Most marine and aquatically deposited coprolites do not show this feature (Schwimmer et al. 2015), but there are examples for coprolites produced by aquatic animals with a flattened surface (Collareta et al. 2019). The flattened specimens in the PDA also lack the cracks indicating drying.

The presence of spiral coprolites in the PDA sample could point to rapid burial, as it has been proposed that spiral faeces must undergo particularly rapid burial in order to retain their original morphology (Northwood 2005).

Morphology

The morphology of the coprolites is highly diverse. It can be influenced by the diet, which may vary by region or periodically change (e.g. through the currently available prey animals or plants (Trites and Spitz 2018)). Alternatively the coprolite shape may vary with the age and life stage of the producer (Bajdek et al. 2017).

The PDA coprolites have been classified into nine morphotypes. For most of them it was not possible to find a clear connection between the recognised morphotype and their producer, because the same animal can produce differently shaped excrements (Chin 2002). Furthermore, some animals produce a scat comprised of differently shaped pellets during a single defaecation event (Diedrich 2012). Only in the case of the spiral morphotype was it possible to narrow down the list of possible producers to fishes with spiral intestinal valves (McAllister 1985; Thulborn 1991; Argyriou et al. 2016). This organ is found in the intestines of Chondrichthyes (sharks, rays) and in some groups of bony fishes, like Dipnoi and some Actinopterygii, for example sturgeons (Acipenseridae) (Hassanpour and Joss 2009; Argyriou et al. 2016). Its function is to slow down the rate of food passage and to enlarge the area of nutrient absorption without the elongation of the intestine itself (Leigh et al. 2021). These groups are represented in the PDA sample by sharks (e.g. *Notorynchus primigenius*, *Squatina* sp., Odontaspididae indet., *Cosmopolitodus hastalis*, *Isurus oxyrinchus*, Lamnidae indet., *Otodus (Megaselachus) megalodon*, *Alopias exigua*, *Anotodus retroflexus*, *Hemipristis serra*, *Galeocerdo aduncus*, *Carcharhinus priscus*, *Sphyrna laevissima*), rays (e.g. Dasyatidae indet., *Aetobatus arcuatus*, *Aetomylaeus* sp., *Myliobatis* sp., *Rhinoptera* cf. *schultzi*) and sturgeons (Acipenseridae indet.) (Szabó et al. 2021).

Within spiral coprolites, it is possible to differentiate between amphipolar and heteropolar specimens based on the location and arrangement of the whorls on the surface (Neumayer 1904; Hunt and Lucas 2012). The coprolite is heteropolar if the closely spaced coils are concentrated at one end, amphipolar if the loosely spaced coils are evenly distributed throughout their length (Hunt and Lucas 2012). The spiral coprolites in the PDA sample are of the heteropolar type. However, whether this classification has taxonomic significance is not known (e.g. Chin 2002).

Turtles cannot be ruled out as producers of the cylindrical-shaped coprolites, as this morphotype has previously been ascribed to these animals (Hunt and Lucas 2012; Bajdek et al. 2019; Brachaniec et al. 2022). However, extant turtle faeces are often soft, irregular or elongated in shape (Balazs et al. 1993; Farlow et al. 2010). The cylindrical morphotype in this paper refers to specimens with a circular cross section, constant diameter and flat ends, whereas coprolites attributed to turtles by Hunt and Lucas (2012) and Bajdek et al. (2019) would have been placed into the elongated morphotype. Therefore, some coprolites belonging to the elongated morphotype might have been produced by turtles.

Producers and prey animals

The most abundant inclusions in the coprolites were derived from fishes. This is easily explained, considering that fishes served as prey for the majority of the aquatic predators recorded at the study site. The most abundant food remains are bony fish vertebrae, which remain unidentifiable taxonomically. Coprolites containing fish teeth with intact enamel were most likely not produced by crocodiles, because the strong stomach acid characteristic for this group is known to decalcify bone and corrode enamel and ganoin (Fisher 1981; Milàn et al. 2012). Bony inclusions in coprolites attributed to turtles appear to be acid-etched, because digestion of extant turtles is characterised by long gut retention time (Bajdek et al. 2019; Barrios-de Pedro et al. 2020a). Despite the fact that no acid etching was observed in the PDA coprolites, it is likely that animals with a highly efficient digestive system, such as crocodiles and turtles, are the putative producers of at least some of the coprolites with a few, or no inclusions. Apart from these taxa, inclusion-free coprolites might have also been produced by predatory animals feeding on soft bodied prey.

The difference in the presence or absence of inclusions in a coprolite was also observed in the thin sections as two clearly different coprofabrics (one with abundant, one without any inclusions) have been identified (see Supplementary Figs. 4–11 and 12–13). These coprofabrics are considered to reflect the diet and the digestive processes (Barrios-de Pedro et al. 2020a) in the way of showing a portion of the diet in the form of food remains, but also the digestive capability in their state of preservation.

Age of the coprolites

The vertebrate remains of Pécs-Danitzpuszta include fossils reworked from sediments of various ages within the Miocene (Sebe et al. 2021a; Botfalvai et al. 2023), thus the coprolites might be of mixed ages as well. In determining the age of a possibly reworked coprolite, we mostly relied on embedded remains with a stratigraphical relevance. Unfortunately, the detectable inclusions from the PDA coprolites were in most cases not indicative of a certain age. The coprolites containing teeth of reef-associated fish (*Calotomus* sp., Labridae) are definitely Badenian, as normal marine conditions necessary for corals were only present during that period in the area (Sebe et al. 2021a). The spiral coprolite morphology, related to fishes like sharks, rays and sturgeons, did not allow separating these coprolites by their age, as both the Badenian cartilaginous fishes and the younger sturgeons produce spiral coprolites.

The surface texture did not help to separate the specimens by their age either, as palaeobiological and taphonomic processes can both produce similar textures. In conclusion, the formation of a surface texture on a coprolite could not be linked to a specific process, but was rather influenced by a series of factors, like the palaeobiology of the animal's digestive system, the habitat, but also by post-depositional processes.

Palynology

It was observed that pollen within each coprolite was dominated by one genus. The analysed samples contain very little organic residue, which is understandable since the coprolites of carnivorous (to a great extent piscivorous) aquatic animals were analysed.

Unfortunately, the palynological analysis of the PDA coprolites was not appropriate for detailed stratigraphical investigation, but provided some information connected to paleoenvironmental reconstruction. An interesting finding was a pollen from the Cichorioideae in the D-2 coprolite, which is far worse preserved than other pollen probably because it may have also passed through the digestive tract of prey (e.g. fish), not only the predator.

Therefore, based on the taxa of pollen preserved in the coprolites, it is possible to estimate air temperature at the time of coprolite production, which ranges from 2.6 to 25.5°C. Coprolite D-4 is from the coldest period (MAT 2.6–15.7°C), whereas coprolite D-6 is from the warmest period (MAT 13.3–18.1°C).

Enrichment of coprolites

At the study site, the abundance of coprolites is exceptional and can be explained by enrichment during the reworking of older sediments (Figure 1). Mechanisms leading to the enrichment of fish osteological remains were discussed by Szabó et al. (2021), and can be accepted for the coprolites as well; they are briefly summarised here.

The accumulation of the coprolite-bearing sands could have been triggered by the coeval rapid uplift of the Mecsek Mts. and/or by climatic changes (Sebe et al. 2021a). The denudation of older Miocene units was a result of subaerial processes in the higher parts of the mountains emerging above the level of Lake Pannon, and of coastal erosion along the lakeshore. The study site is located just in front of the marginal fault along which the range was uplifted, thus it received a large amount of sediment input from the high-relief background. Most of the coarse sediment was deposited very close to the lakeshore, exactly where the studied outcrop lies, this could have contributed to the selective deposition of fossils. The fine fractions of the eroded siliciclastic sediments could have been winnowed out by wave action, while carbonate rocks could have also been dissolved. All these processes helped to enrich the density of coprolites in the host sediment.

Conclusions

There is an abundant coprofauna known from the Neogene Pécs-Danitzpuszta sand pit in Hungary. The locality is unique among Miocene coprolite bearing localities for the large number of vertebrate coprolites found. The fossils contained mostly fish related inclusions, such as vertebrae, scales and teeth of three identifiable taxa (Sparidae indet., Labridae indet. and *Calotomus* sp.). Apart from these, fossilised remains of molluscs, ostracods and a gastropod were observed. The coprolites were probably produced by aquatic piscivores. The producers of the spiral morphotype were fishes with spiral intestinal valves. The exact age of most of the coprolites remains a question, but there are certainly Badenian specimens, based on geologic age-specific teeth found within them belonging to reef associated fish.

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Disclosure statement

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